Size, site fidelity, and overlap of home ranges and core areas in the socially monogamous Owl monkey (Aotus azarae) of northern Argentina

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Abstract

In addition to environmental factors, social variables such as group size may play an important role in explaining primate ranging patterns. In this study we investigated range sizes, site fidelity and range overlaps of owl monkeys (*Aotus azarae)* in Northern Argentina. We calculated the size of home range and core areas for 18 groups in our study area. For the six most intensively studied groups we tested whether precipitation as a crude proxy for food availability or group size had an influence on range size, assessed the degree of site fidelity by quantifying overlaps of annual ranges and core areas and calculated the amount of range overlap between neighboring groups for each year. We used the kernel density estimation method to calculate home ranges as 90% kernel and core areas as 50% kernel. Home range size (mean ± s.d.) was 6.2 ha (± 1.8) and core area size 1.9 (± 0.6). Rainfall and group size were not statistically significant predictors of range sizes. Site fidelity was high with a range overlap of 82% (± 11) between consecutive years. Neighboring groups overlapped over 48% (± 15) of the outer parts of their group ranges and 11% (± 15) of their core areas. We found no evidence that larger groups occupy larger areas than smaller groups, suggesting that food availability might be above a critical threshold for owl monkeys so that larger groups do not need to extend their foraging areas to meet their energy requirements. Our findings indicate that ranges remain stable over several years as groups visit the same locations of fruit trees within their range. We showed that owl monkeys exhibit a considerable degree of range overlap. However, we suggest that this range overlap might be spatial rather than temporal, which maximizes access to clumped feeding resources in overlapping areas that are used at distinct times, while excluding other males from access to females in exclusively used areas.

Keywords: Home range; core area; site fidelity; kernel density estimation; social monogamy; territoriality; *Aotus azarae*

Introduction

Space use is an important aspect of primate behavior that is often described using the concepts of home range and core areas. The home range is defined as "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young" (Burt 1943, p. 351), whereas the core area delineates areas more intensively visited within the overall home range (Boitani and Fuller 2000). Different factors influence space use among primates. Ranging is, for instance, directly linked to metabolic expenditure and body size (Clutton-Brock and Harvey 1981; Dobson et al. 2010; Lehman et al. 2007; Milton and May 1976). Additionally, the availability of different resources has also been shown to influence individual spatial behavior. While the location of water or sleeping sites may affect the use of space (Zhou et al. 2011), the diet, quality and distribution of food sources are usually considered the most important resources influencing patterns of ranging (Buzzard 2006). Generally, folivorous primates have smaller ranges as they exploit ubiquitous food resources, while frugivorous and insectivorous primates have comparatively larger ranges and longer daily travel distances to exploit unpredictable or patchily distributed resources (Clutton-Brock and Harvey 1977b). When preferred food sources become scarce, primates exhibit dietary responses by increasing the amount of fallback foods in their diet and by reducing their daily travelled distances (Brockman and van Schaik 2005; Fernandez-Duque et al. 2013; Zhang 1995) which is subsequently reflected in changes in range size.

In many primate species, home range size is also related to group size, in line with the prediction that groups will expand their range when the number of individuals in a group increases if scramble-competition is present (Clutton-Brock and Harvey 1981; Isbell et al. 1998; Watts 1998). Thus, larger groups have been observed to expand their ranges when food is limited, to compensate for increasing competition with other group members (Clutton-Brock and Harvey 1977a; Dias and Strier 2003; Teichroeb and Sicotte 2009). This has, for example, been documented in vervet monkeys (*Cercopithecus aethiops,* Isbell et al. 1998), mountain gorillas (*Gorilla gorilla beringei*,

69 Watts 1998), chimpanzees (*Pan troglodytes,* Herbinger et al. 2001), black and gold howler (*Alouatta*
70 *caraya*, Agostini et al. 2010) and tufted capuchin monkeys (*Cebus apella nigritus,* Di Bitetti 2001).
71 However, in some primate taxa there seems to be no relationship, such as in the blue-eyed black
72 lemur (*Eulemur flavifrons,* Sylviane et al. 2011) and Thomas's langur (*Presbytis thomasi*, Steenbeek
73 and van Schaik 2001).

74 Other factors that affect range use in group-living primates are the needs to defend mating
75 partners, offspring or food resources from neighboring groups (Fashing 2001; Garber et al. 1993;
76 Lazaro-Perea 2001). Territorial behavior is expected to evolve when resources are both limited and
77 defendable (Mitani and Rodman 1979). Defendability depends on the size of the overall range, the
78 length of its boundary, detection distance and the ability of individual groups or sub-groups to patrol
79 the borders of a territory (Lowen and Dunbar 1994). Territorial behaviors in primates, such as
80 vocalizations (Cowlishaw 1992), boundary controls (Mitani and Watts 2005) and aggressive
81 encounters with neighboring groups (Wilson et al. 2001), are well documented, yet few studies have
82 analyzed the spatial components of territoriality (e.g. Markham et al. 2012; Williams et al. 2002).
83 Despite inter-group competition due to limiting factors, numerous species, including some territorial
84 ones, show overlapping zones between the home ranges of neighboring groups (Biebouw 2009;
85 Sylviane et al. 2011). These overlapping zones are generally under-used (Wrangham et al. 2007).

86 Most of the analyses mentioned above have focused on relatively short periods of a few
87 seasons or years. Few studies of primate ranging behavior cover temporal scales that allow the
88 detection of long-term characteristics of ranging behavior, like range shifts or site fidelity. Those
89 that have include for instance, long-term studies of a population of ring-tailed lemurs (*Lemur catta*),
90 which found that troops remained site-faithful during three decades (Jolly and Pride 1999; Mertl-
91 Millhollen 2000). Another study, which documented high site fidelity of gray-cheeked mangabeys
92 (*Lophocebus albigena*) during a decade, found that range shifts were linked to dispersal of
93 individuals or group fission (Janmaat et al. 2009). Possible reasons for site fidelity are the benefits

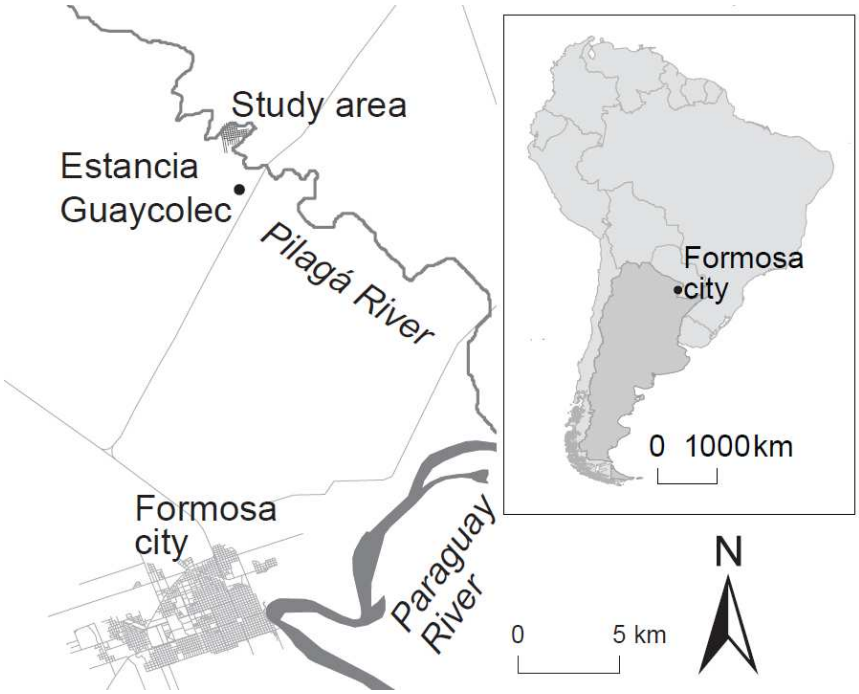
94 derived from knowing the location of important resources such as sleeping sites, feeding trees or
95 efficient travel routes. Consequently, movement into unknown areas may be associated with
96 increased costs, as, for example, in vervet monkeys (*Cercopithecus aethiops*, Isbell et al. 1990).
97 Moreover, most studies of home ranges in primates have not taken into account differential space
98 use or have not quantified the size of overlapping zones. Those which have mainly focused on
99 examining the conditions under which overlapping ranges may be more likely, costly or adaptive
100 (Mitani and Rodman 1979; Nievergelt et al. 1998; Wrangham et al. 2007), rather than empirically
101 analyzing the use patterns of these shared space in comparison with more exclusively used areas
102 (Benadi et al. 2008; Wartmann et al. 2010). To investigate the degree of range overlap is especially
103 relevant for understanding the evolution of primate social systems (Lukas and Clutton-Brock 2013).
104 The mate-guarding hypothesis for the evolution of social monogamy in mammals predicts that when
105 females occupy small, discrete ranges, males are unable to defend several females from other mating
106 partners, and may form a pair with one female whom they guard from other male competitors
107 (Komers and Brotherton 1997). Under this hypothesis, it is proposed that non-overlapping territories
108 may be a prerequisite for social monogamy to evolve.
109 In this study we chose a socially monogamous primate, the Azara's owl monkey (*Aotus*
110 *azarae azarae*) of the Argentinean Chaco to describe long-term home range sizes, and to study
111 social factors influencing ranging behavior. Owl monkeys (*Aotus* spp.) are distributed over a wide
112 geographic area that extends from Panamá to the South American Chaco (Fernandez-Duque 2011a).
113 These small arboreal primates live in groups that generally consist of an adult reproductive pair, one
114 infant, and one or two juveniles and subadults (Fernandez-Duque 2011a; Wright 1994). Owl
115 monkeys are socially monogamous (Fernandez-Duque 2011b), with males showing intense care of
116 infants (Fernandez-Duque et al. 2009; Huck and Fernandez-Duque 2013). Natal dispersal of both
117 males and females usually occurs when individuals are approximately three years old (Fernandez-
118 Duque et al. 2009). Like other owl monkey species, Azara's owl monkeys are primarily frugivorous

(Fernandez-Duque 2011b). Unlike all other owl monkey species, which are strictly nocturnal, Azara's owl monkeys are cathemeral (Tattersall 2006), being active as much during the day as during the night (Erkert et al. 2012; Fernandez-Duque et al. 2010).

Across their continental distribution, all species have relatively small home ranges that vary between four and ten hectares (Fernandez-Duque 2011b). Owl monkeys, including *Aotus azarae,* have been observed to show forms of territorial behavior during inter-group encounters, varying from ritualized displays and vocalizations with no physical contact to chases and fights which may include violent physical contact between members of different groups (Wright 1978, pers. observations of the authors). Despite these territorial behaviors, owl monkey groups have been sometimes observed to use the same areas, suggesting overlapping ranges. However, there has been some debate on the extent of overlap between neighboring ranges: whether they overlap extensively (Wright 1978) or only slightly (Fernandez-Duque 2011b).

We present here the results of a 10-year study that examined the home ranges of 18 groups of owl monkeys in Formosa, Argentina. For six of the groups we also evaluated whether there was a relationship between annual range size, precipitation as a crude proxy for food availability and group size, how much the outer range portion of their ranges and the areas of more intense use within the range (core areas) changed across years and which parts of these ranges overlapped with neighboring groups. For our study we made the following predictions: first, we expected to find a difference in ranging between relatively large groups (5-6 individuals) and smaller ones that may be a response to scramble competition, and we expected annual range sizes to remain stable as long as group size remains unchanged. We tested these predictions by assessing the relationship between group sizes and ranging patterns and evaluated whether larger groups overlapped more with neighboring groups more than smaller ones. Second, we assumed that for primarily frugivorous primates, knowledge of the location of fruit trees and time of fruiting is essential to exploit patchily distributed resources. Since we had observed that groups frequently re-visit feeding trees within

144 their range, we thus predicted that ranges would remain relatively stable over several years. We
145 tested this prediction by quantifying site fidelity as the degree of overlap between annual ranges.
146 Finally, under the mate-guarding hypothesis (Komers and Brotherton 1997) we expect non-
147 overlapping territories that are actively defended. To test this prediction we quantified the degree of
148 range overlap to evaluate whether owl monkey ranging patterns provide support for the mate-
149 guarding hypothesis. We predicted that range overlap would be less than 21%, the reported mean for
150 26 socially monogamous primate species (Lukas and Clutton-Brock 213). We expected groups with
151 larger annual ranges and core areas to have higher overlapping areas, because of the constraints to
152 defend larger ranges.
153
154 **Methods**
155 *Study area and population*
156 The study area is located in the cattle ranch Estancia Guaycolec (S 25.9735 / W 58.1913),
157 approximately 25 kilometers north of the city of Formosa in Northern Argentina (Fig. 1).



158
159 **Fig. 1** Location of the study area in "Estancia Guaycolec" ranch in Formosa Province, Argentina

The ranch includes a mosaic of grasslands and savannas, semi-deciduous gallery forest along the banks of the Pilagá river (Placci 1995) and isolated patches of forests immersed in the savanna matrix. The owl monkey groups inhabit both the gallery forest and the isolated patches (Juárez et al. 2012). Within the gallery forest, a system of transects that runs east to west and north to south, spaced every 100 m, covers an area of approximately 300 hectares. Transects are marked every 50 m with fluorescent plastic flagging and aluminum tags. We georeferenced these points with GPS to allow easy and reliable recording of location data of marked transect points. Placci (1995) and van der Heide et al. (2012) thoroughly characterized the structure, composition and phenology of the gallery forest. The owl monkey groups inhabiting the 300 ha area are habituated to researchers as Fernandez-Duque et al. (2001) have been monitoring them since 1997.

We considered sixteen neighboring groups and two peripheral ones in the vicinity of the study area for the analyses of long-term home range and core area size. There are no other non-study groups in the area occupied by the 18 groups we studied. Six neighboring groups (C0, Cola Corta, D100, D500, E500, E350) that have been more intensively studied since 1997 contributed most of the spatial data for the analyses of annual ranging patterns. The number of groups in the area did not change during the study. More detailed analyses of demographic and life-history data for the study population can be found elsewhere (Fernandez-Duque 2009; Huck and Fernandez-Duque 2012; Huck et al. 2011; Juárez 2012).

Long-term home ranges and core areas

We calculated long-term home ranges for all 18 groups using data from 1998-2008. We contacted groups in the population at least once a month. Given the cathemeral habits of the species (Fernandez-Duque et al. 2010), we contacted the groups during active periods that take place early in the morning (0500-0930 hrs) and late in the afternoon (1600-2130 hrs). When we contacted a

group, we observed it for a minimum of 15 minutes and collected data on group composition. A more detailed description of demographic data collection is presented elsewhere (Fernandez-Duque 2009). We also recorded the group's location in relation to the georeferenced transect system. Later, we estimated the latitude/longitude coordinates for the recorded location with a spreadsheet formula using the distance, angle and the GPS position from the tagged and georeferenced transect point. We tested this method of ranging data collection by comparing locations for points collected with compass and with a GPS device (Garmin Oregon™ 200, Garmin International Inc, Olathe, KS, USA) and found that the method using georeferenced transect points provided an accuracy of approximately 10 m per location; acceptable for the questions being explored in our study.

For long-term home range calculations, 8177 locations were available from the 18 studied groups (Table 1). The number of locations varied among years, months and groups. We obtained a mean (± s.d.) of 145 (± 24) locations per year. The least sampled year was 1998 at the beginning of the study period (167 locations), and the most sampled one was 2008 (1596 locations). We obtained a mean of 42 (± 26) locations per group per year.

Table 1. Yearly sample sizes of recorded locations for 18 owl monkey (*Aotus azarae*) groups in "Estancia Guaycolec" ranch, Formosa Province, Argentina, 1998-2008.

	Year											
Group	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Total per group
A500	0	0	0	0	6	4	4	2	4	10	24	54
A900	0	1	10	6	6	10	37	16	2	4	6	98
B69	16	64	52	46	82	66	39	18	10	16	10	419
C0	39	84	45	58	84	79	102	85	16	42	157	791
CC	27	89	56	47	154	89	117	59	11	44	166	859
Colman	0	0	0	17	146	88	109	59	10	18	98	545
D100	23	71	46	83	34	78	83	85	22	48	179	752
D1200	5	19	19	50	102	46	62	10	6	7	12	338
D500	29	61	60	149	180	104	95	67	31	31	171	978
D800	1	46	70	40	26	28	110	35	12	16	84	468
E350	0	0	0	0	0	103	95	116	39	46	218	617
E500	22	41	44	87	155	51	70	53	16	42	237	818
F700	0	0	5	1	62	57	49	22	12	8	50	266
F1200	5	18	26	15	63	96	80	61	12	16	86	478
G1300	0	0	0	0	42	74	67	59	18	4	26	290
IJ500	0	13	7	5	9	50	26	4	2	6	21	143
L100	0	0	0	0	2	12	18	35	16	6	37	126
Veronica	0	0	0	0	2	48	19	42	4	8	14	137
Total per year	167	507	440	604	1155	1083	1182	828	243	372	1596	8177

Throughout the study period, April was the least (467 locations) and October the most sampled month (925 locations), and we obtained a mean of 38 (± 7) locations per group per month. The group A500 was the least sampled group and D500 the most. In order to reduce the potential influence of different sampling intensities across groups and time, and to reduce the amount of autocorrelation present in data sets with high sample sizes (Swihart and Slade 1985) we chose a random subset of 800 locations for groups with more than 800 locations as an optimal balance between reducing amounts of autocorrelation while retaining as much biologically meaningful

212 information as possible. For subsampling we used Hawth's analysis tools (Beyer) in ArcGIS 9.1
213 (ESRI Inc., Redlands, CA). In total we retained 7400 locations for analysis.
214 To estimate the size of the home ranges, we used the kernel density estimation (Worton
215 1989); currently the prevalent method in wildlife biology to calculate home ranges (Laver and Kelly
216 2008). The kernel density estimation (KDE) provides a probabilistic measure of how animals use
217 space and allowed us to distinguish between areas of different intensities of use (Horne and Garton
218 2006), which for example is not possible with the Minimum Convex Polygon method (Wartmann et
219 al. 2010). We used the fixed kernel density estimation method as implemented in the home range
220 tools extension HRT (Rodgers et al. 2007) in ArcGIS with a raster resolution size of 150 m. This
221 raster resolution provided adequate results given the size of the home ranges we were calculating,
222 without being too computationally intensive. One of the limitations of the kernel method is that it is
223 sensitive to the choice of the smoothing parameter, or bandwidth (Gitzen et al. 2006). Various
224 methods are available to select the smoothing parameter objectively (Kernohan et al. 2001). We
225 used biased-cross validation for smoothing parameter selection because, compared to other
226 smoothing parameter selection methods, such as Least-Squares Cross Validation, it is stable at large
227 sample sizes (Hemson et al. 2005; Wartmann et al. 2010). The mean (± s.d.) of all smoothing
228 parameters calculated for home range estimates was 0.38 (± 0.06, N = 18). We report home ranges
229 based on 90% volume contours of kernel probability density surface, since the 95% curve is less
230 accurate (Börger et al. 2006). As most home range studies employing KDE calculated core areas
231 based on 50% volume contours (Laver and Kelly 2008), including primate ranging studies
232 (Williams et al. 2002), we employed the same measurement. To assess the accuracy of the fixed
233 kernel density estimation, we visually compared the spatial distribution of the original locations with
234 the home range as estimated by the model. All kernel estimates fitted the distribution of the original
235 locations well, except for one group (Colman). This group lives in an isolated, narrow island of
236 forest surrounded by grassland outside the main area of study. Because of the relatively narrow and

linear shape of this island of forest, the estimation established the home range boundary outside the area where the group actually ranges. Thus, for this group, we manually adapted the smoothing parameter to h=0.1 to produce a more conservative home range estimate. All results are presented as means with standard deviation (± s.d.).

Variation in annual ranges, core areas and group size

To analyze ranging patterns at smaller temporal scales of years, we calculated annual ranges and core areas for the six intensively studied groups. We used the same kernel density estimation method to calculate annual ranges as described for the long-term home ranges above. The number of recorded locations varied among groups and years. Thus, for the calculation of each annual range, we chose a random subset of 100 locations if the total number exceeded 100 locations. When we had less than 35 locations available for a certain group and year, we did not estimate a range for that year. To ensure that the number of locations did not have an influence on range estimates, we used Spearman's correlation in PASW 18 (SPSS Inc., IBM Corporation NY) to evaluate the relationship between the total number of locations used to calculate a range and the resulting range size for both annual ranges and core areas. The relationship was weak and not statistically significant for annual ranges (Spearman's rho=0.091, P=0.512, N=54) or for core areas (Spearman's rho=0.126, P=0.363, N=54). The mean (± s.d) of smoothing parameters used to estimate annual ranges and core areas was 0.47 (± 0.04, N = 54 smoothing parameters). We used One-Way ANOVA to test whether there were statistically significant differences among groups in annual ranges, core areas and group size. We tested the relationship between annual range and core area sizes and changes in group size with Spearman's correlation tests using data on group size for January-February of each year. We chose group size in January-February because it is a time when demographic events that change group size are less likely; births are concentrated in October-December (Fernandez-Duque 2002), dispersals in August-December (Fernandez-Duque 2009) and replacements of adults in April-June (Huck and

Fernandez-Duque 2012). We used general linear mixed models to determine if the dependent variables "annual range" and "core area" were related to rainfall and group size (fixed effects), including group identity as a random factor.

Site fidelity

To assess the degree of site fidelity, we analyzed the extent of areas which owl monkeys used repeatedly over time. We tested for site fidelity for annual ranges, as well as for core areas, by calculating the intersection of kernel contours for consecutive years in ArcGIS. To test for possible long-term range shifts, we calculated the amount of range overlap between the annual range in 1999 for each group with the annual range of the same group in 2008 (e.g. overlap of range in 1999 with range in 2008 for the group Cola Corta) and repeated this calculation for core areas.

Overlaps of annual ranges and core areas between neighboring groups

To quantify the degree of range overlap between owl monkey groups we calculated the extent of each group annual range that overlapped with the ranges of neighboring focal groups. We only calculated range overlap between focal study groups, and not between focal and non-focal groups, although there is also some additional overlap with those. Using both annual ranges as outer range boundaries, as well as delineations of core areas, we were able to also consider internal space use patterns. We calculated overlaps for the annual range and for the core area as the size of the polygons formed by the intersection of the respective kernel contours in ArcGIS. The sample sizes reported correspond to the number of pairs of years that were compared. We tested whether larger groups overlapped more with neighboring groups more than smaller ones by assessing whether there was a relationship between the size of annual ranges and core areas and the size of overlapping areas using Spearman's correlation.

Results

Long-term home ranges and core areas

The mean home range size was 6.2 ha (± 1.8 ha, N=18) between 1998-2008. The largest home range was three times as large as the smallest one (Veronica: 10.9 ha vs. D500: 3.6 ha, Fig. 2, Table 2). The mean core area size was 1.9 ha (± 0.6, N=18) and the range was relatively smaller (1.0-2.6 ha, Table 2).

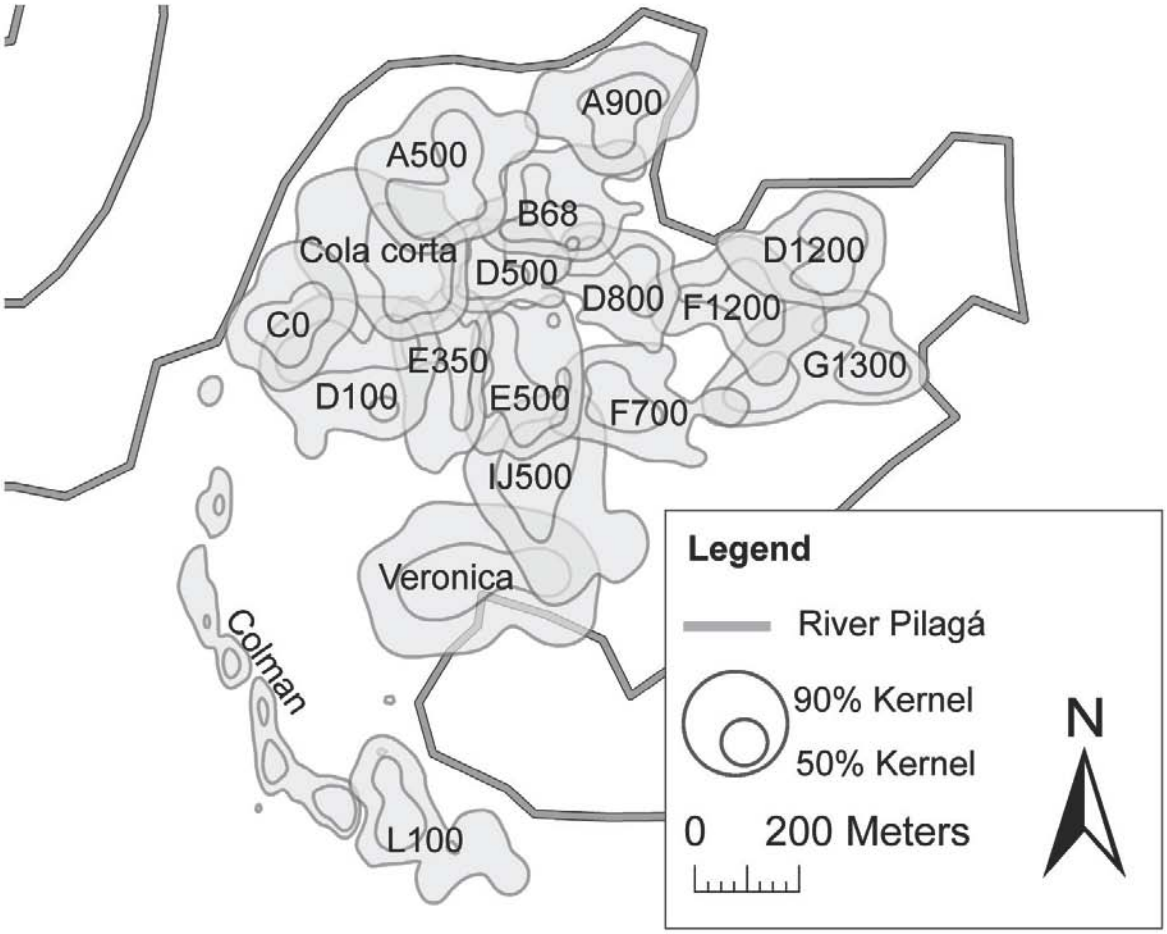


Fig. 2 Owl monkey home ranges and core areas of the 18 study groups in "Estancia Guaycolec" ranch in Formosa Province, Argentina, 1998 – 2008

Table 2. Home ranges and core areas of 18 owl monkey (*Aotus azarae*) study groups in "Estancia Guaycolec" ranch, Formosa Province, Argentina, 1998-2008

Group	Home range (ha)	Core area (ha)
A500	7.2	2.6
A900	5.8	1.7
B68	5.2	1.6
C0	5.1	1.6
Cola corta	8.2	2.6
Colman	4.4	1.0
D100	8.0	2.5
D1200	5.1	1.6
D500	3.6	1.2
D800	4.3	1.3
E350	5.3	1.8
E500	5.8	2.3
F700	5.2	1.4
F1200	5.7	1.7
G1300	7.3	2.7
IJ500	9.1	2.6
L100	5.4	1.2
Veronica	10.9	3.2
Mean	6.2	1.9
s.d.	1.9	0.7

Variation in annual ranges, core areas and group size

The mean annual range was 6.0 ha (± 2.2 ha, N=6 groups) and groups differed markedly in the size of their annual ranges (One-way ANOVA: df=5, F=18.8, P<0.001, Table 3, Fig. 3). For example, D500 with a mean annual range size of 3.8 ha (± 0.4 ha, N=10 years) consistently occupied less than half the range of D100 (8.4 ha ± 1.9, N=8) or Cola Corta (8.2 ha ± 1.6, N=9). The mean core area was 1.9 ha (± 0.7, N=6 groups), and groups also differed markedly in the size of those (One-way ANOVA: F=17.74, df=5, P<0.001).

There was no significant within-group variation in the size of the annual ranges across years (Table 3, One-way ANOVA: F=0.738, df=10, P=0.685).

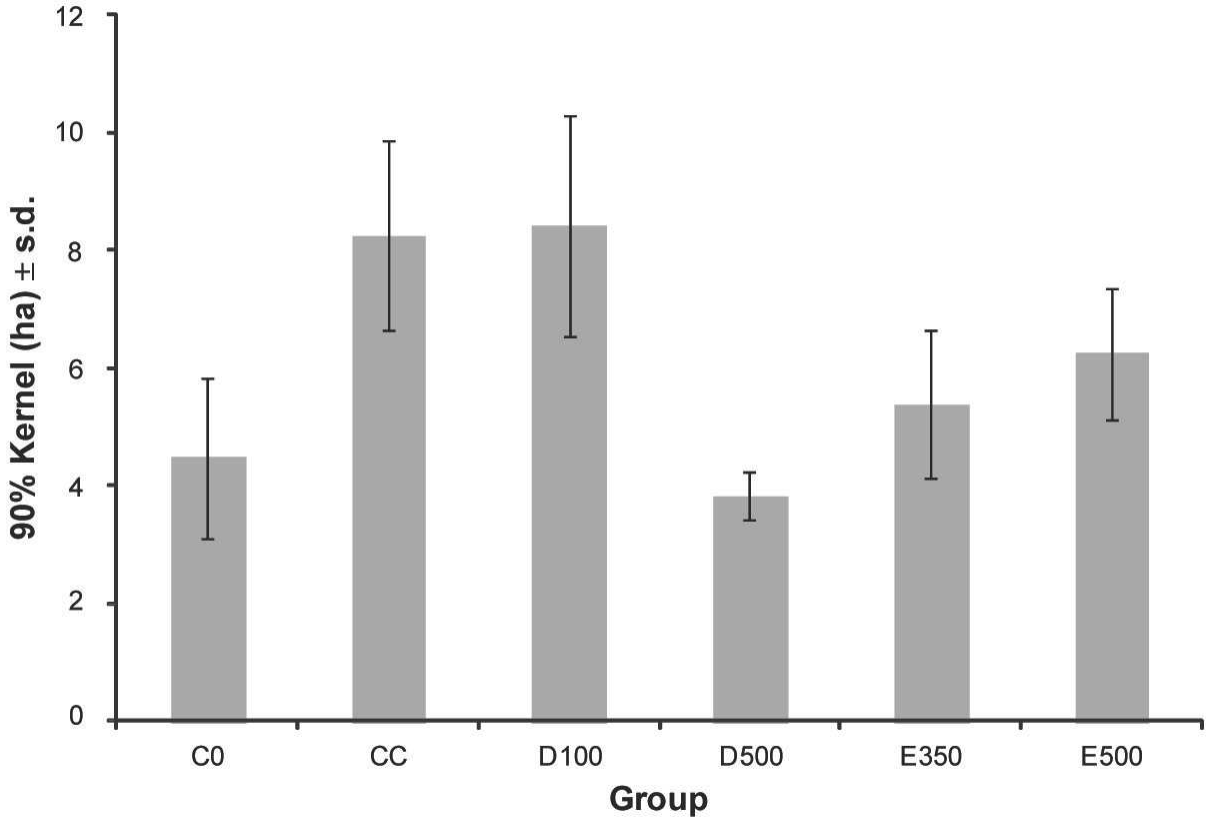


Fig. 3 Owl monkey mean annual ranges for the six focal study groups in "Estancia Guaycolec" ranch in Formosa Province, Argentina, 1998 – 2008

Table 3. Annual ranges (ha) for six focal study groups of *Aotus azarae* in "Estancia Guaycolec" ranch, Formosa Province, Argentina from 1998 - 2008.

Year	Group	C0	Cola Corta	D100	D500	E350	E500	Mean annual range (ha)	s.d.
1998	3.5	-	-	-	-	-		3.5	0.0
1999	5.0	7.3	8.0	3.5	7.7	7.4		6.5	1.8
2000	3.1	6.7	8.1	3.3	5.2	8.3		5.8	2.3
2001	3.3	12.1	12.2	4.0	-	6.5		7.6	4.3
2002	7.2	7.6	-	4.3	-	5.2		6.1	1.6
2003	5.7	7.1	8.4	3.8	4.5	4.9		5.7	1.7
2004	5.5	8.1	9.9	4.5	5.5	6.6		6.7	2.0
2005	4.0	7.9	7.3	4.2	6.3	5.6		5.9	1.6
2006	-	-	-	3.4	4.7	-		4.1	0.9
2007	3.1	8.5	6.7	3.6	3.5	5.4		5.1	2.1
2008	4.2	8.9	6.6	3.6	5.7	6.0		5.8	1.9
Mean	4.5	8.2	8.4	3.8	5.4	6.2		6.0	
s.d.	1.4	1.6	1.9	0.4	1.3	1.1		2.2	

Mean group size was 3.6 individuals (± 1.0, N=6 groups, Table 4). Differences in size among groups were pronounced and statistically significant (Table 4, One-way ANOVA: F=2.8,

df=5, P=0.026). The group Cola Corta was consistently the largest group (4.2 ± 0.8, N=10 years), whereas D100 was the smallest one (2.9 ± 0.6, N=10).

Table 4. Group size of six focal study groups of owl monkeys (*Aotus azarae*) in "Estancia Guaycolec" ranch in Formosa Province, Argentina in January of each year, 1998-2008.

	Year												
Group	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Mean	s.d.
C0	5	4	5	4	4	2	3	2	2	2	2	3.2	1.3
Cola Corta	-	5	5	4	5	3	3	4	4	4	5	4.2	0.8
D100	-	3	4	3	2	3	2	3	3	3	3	2.9	0.6
D500	-	3	3	4	4	5	6	3	3	4	4	3.9	1.0
E350	-	3	3	3	-	2	3	4	4	4	4	3.3	0.7
E500	-	-	5	5	3	2	3	4	5	5	3	3.9	1.2

Neither annual range or core area size were significantly related to group size (Table 5).

Table 5. Spearman's rho for the correlation of group size and annual range/core area for six focal owl monkey (*Aotus azarae*) study groups in "Estancia Guaycolec" ranch, Formosa Province, Argentina, 1998-2008.

	Annual Range			Core Area		
Group	rho	p	n	rho	p	n
C0	-0.25	0.478	10	-0.25	0.490	10
CC	-0.16	0.680	9	-0.61	0.084	9
D100	-0.22	0.604	8	-0.44	0.280	8
D500	0.63	0.049	10	0.39	0.259	10
E350	0.39	0.927	8	-0.20	0.642	8
E500	0.50	0.206	8	0.45	0.263	8

Neither rainfall nor group size were strong predictors of the annual range (rainfall, $F=3.291$, $P=0.192$; group size, $F=1.2$, $P=0.272$) or the core area (rainfall, $F=0.279$, $P=0.606$, group size, $F=0.509$, $P=0.480$). However, the variable "group" was highly predictive of the annual range ($F=18.68$, $P<0.001$) and core area ($F=4.777$, $P<0.001$) suggesting that most of the observed variation in range sizes was explained by variation among individual owl monkey groups.

Site fidelity

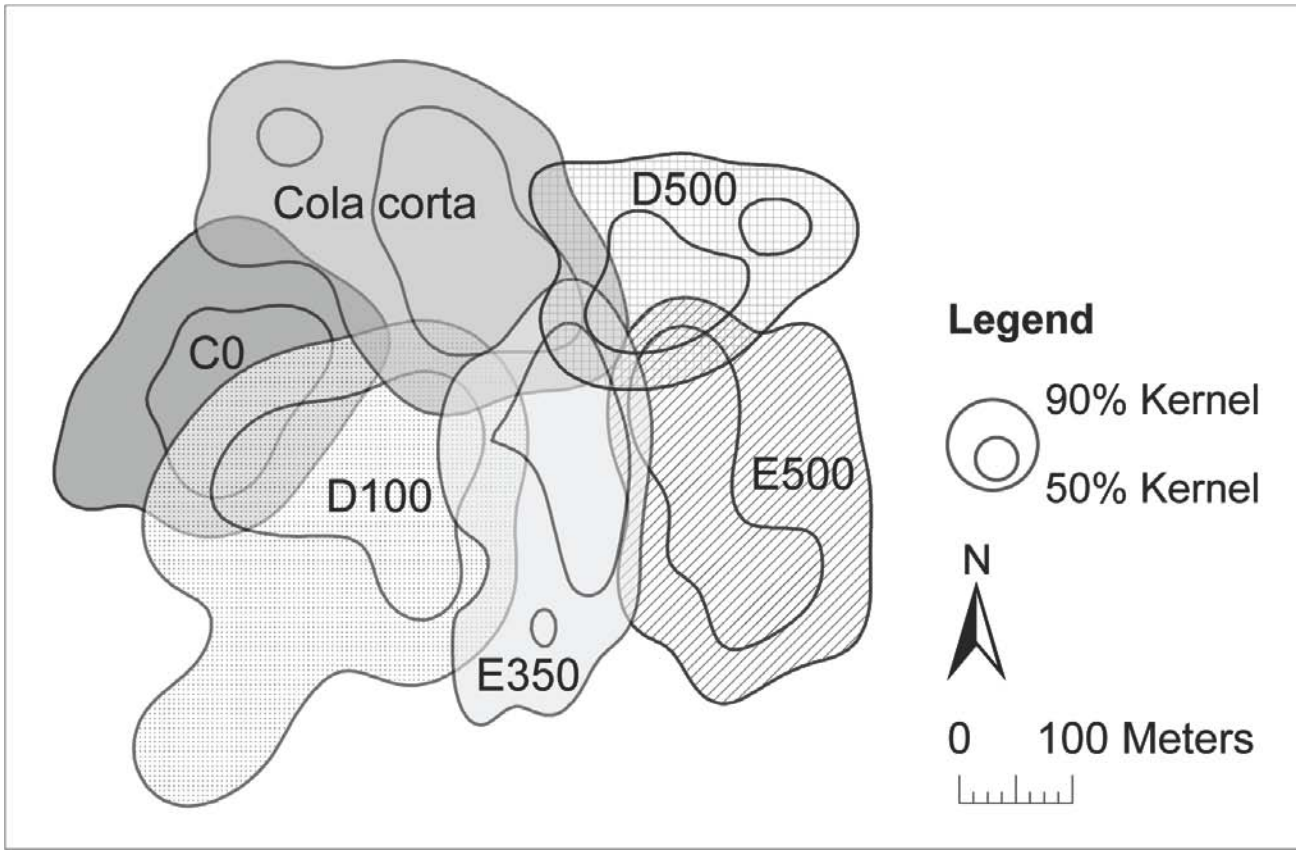
Site fidelity in owl monkeys was high; ranges remained fairly stable during almost a decade. We found a mean overlap between outer range boundaries of successive years of 82% (± 11, N=6 groups, Table 6). The highest mean overlap was 86% and the lowest 78% (Table 6). The highest annual range overlap between two successive years was 98% and the lowest 54%. For core areas, the average overlap between successive years was 65% (± 15, N=6 groups, Table 6). The highest

360 mean overlap was 71% and lowest 60% (Table 6). The highest core area overlap between two
361 successive years was 100% and the lowest 34%.
362
363 **Table 6.** Mean and standard deviation of core area and annual range overlap (%) for six
364 focal study groups of owl monkeys (*Aotus azarae*) in "Estancia Guaycolec" ranch, Formosa
365 Province, Argentina, 1998 – 2008. N=number of comparisons between successive annual ranges.
366

Group	N	Mean core area	s.d.	Mean annual range	s.d.
C0	7	62	11	78	15
Cola Corta	7	71	20	84	14
D100	5	72	8	86	8
D500	6	60	14	85	5
E350	3	62	14	85	17
E500	6	64	21	78	7
Total	34	65	15	82	11

367
368 Mean overlap was 77% (± 19, N=6) between the annual ranges in 1999 and those occupied
369 in 2008. The highest annual range overlap was 99% and the lowest was 62%. The mean overlap of
370 core areas was 47% (± 25, N=6), the highest was 84% and the lowest 16%.
371
372 *Overlaps between annual ranges and core areas of neighboring groups*

373 Groups overlapped considerably in the outer parts of their ranges (Fig. 4). On average,
374 almost half of a focal group's annual range overlapped with neighboring focal groups (48% ± 15).
375 There was also variation among groups in the range of overlap. The groups that shared, on average,
376 the smallest parts of their range were Cola Corta (41% ± 25, N=8 years) and D100 (43% ± 5, N=8),
377 whereas the largest mean overlaps were observed for C0 (54% ± 15, N=8) and E350 (56% ± 6,
378 N=5).
379



380

381 **Fig. 4** Owl monkey group annual ranges, core areas and overlaps for the six focal study groups in
382 "Estancia Guaycolec" ranch in Formosa Province, Argentina. Data for 2004 are displayed as an
383 example.
384

385 Groups with larger annual ranges overlapped more with neighboring groups than groups
386 with smaller ranges (Spearman's rho=0.63, P < 0.001, N=34). However, we found no evidence that
387 larger groups overlapped more with other groups than smaller ones (rho=0.13, P=0.475, N=34).
388 The extent of overlap of the core areas was much smaller (11% ± 15), but the variation
389 among groups was still pronounced. For example, there was almost exclusive use of the core area by
390 Cola Corta (1% ± 1, N=8 years) and E500 (2% ± 4, N=5), whereas C0 and D100 overlapped on
391 average almost a fifth of their core areas with other groups (C0: 17% ± 12, D100: 18% ± 23). We
392 did not find that groups with larger core areas had larger parts of their core areas overlap with
393 neighbors (rho=-0.1, P=0.574, N=34). There was also no relationship between the amount of overlap
394 and group size (rho=0.01, P=0.942, N=34).
395
396 **Discussion**
397 *Inter- and intraspecific variation in owl monkey home ranges*
398 Our study provides some new findings on space use by Azara's owl monkeys of the
399 Argentinean Chaco. Focusing on a large number of identified groups intensively sampled during a
400 decade, our data show that owl monkey groups occupy home ranges that average six hectares and
401 include a core area that is approximately two hectares. These estimates of home range size are in
402 good agreement with previous estimates of 4 to 12 ha for the same population (Fernandez-Duque
403 2011b), for two other populations inhabiting isolated patches of forest in the region (Juárez 2012)
404 and for a different subspecies (*A. a. boliviensis*, 10 ha, N=1 group, García and Braza 1987).
405 Estimates of home range size for other tropical owl monkey species have also reported sizes within
406 this range: *Aotus nigriceps* groups occupy 4-17 ha in Manú NP, Peru (N=3 groups, Wright 1994),
407 and *A. vociferans* of 6 ha in Yasuní, Ecuador (N=1, Fernandez-Duque et al. 2008a). That all owl
408 monkey species, strictly nocturnal or cathemeral, tropical or subtropical, in continuous or

409 fragmented landscapes, seem to occupy ranges of similar size suggests influences that exceed the
410 merely ecological ones.

411 Comparing different populations, subspecies and species is a powerful approach to identify
412 ecological factors influencing patterns of use of space. In fact, much of comparative primate
413 socioecology has been developed by comparing data from different species in various habitats to
414 investigate the influence of those habitats on the behavioral ecology of the species under
415 consideration. However, comparative studies are complicated by differences in sampling strategy,
416 sample sizes and home range models. Most studies quantifying home ranges in *Aotus spp*. have used
417 Minimum Convex Polygon (MCP) methods on a relatively small number of groups sampled during
418 time intervals of several months or few years. MCP methods have the undesirable tendency to
419 underestimate ranges at low sample sizes and to overestimate them at higher sample sizes (Burgman
420 and Fox 2003; Wartmann et al. 2010), whereas kernel estimates are much less susceptible to sample
421 size (Kernohan et al. 2001; Wartmann et al. 2010). In order to be able to conduct comparative
422 studies in the future, researchers should use standardized methods to estimate ranges and report the
423 model and methods used carefully (Laver and Kelly 2008; Sterling et al. 2000). Our results illustrate
424 an impressive range of variation; some home ranges were three times as large as others. This intra-
425 population variation exceeds the reported inter-species variation.

426

427 *Variation in annual ranges, core areas and group size*

428 We found no significant within-group variation in mean annual range size. This may explain
429 why we found no within-group relationship between range size and environmental or social factors
430 such as rainfall or group size. However, it seems likely that food availability might influence owl
431 monkey ranging on smaller temporal and spatial scales than we assessed in this study. For example,
432 future studies should investigate whether ranging patterns vary between the dry and wet seasons.

433 We found significant between-group variation in the size of ranges used. Variability in the
434 size of core areas between groups was lower, but still pronounced. We predicted that variation in
435 group size would be related to differences in range sizes; larger groups ranging over bigger areas
436 than smaller ones. However, our data do not support this prediction, as the number of individuals in
437 owl monkey groups was not significantly associated with the size of the annual range or core area.
438 An earlier study (Fernandez-Duque et al. 2013) suggested that food availability in core areas is
439 above a critical threshold necessary for owl monkeys; thus larger groups may not need to expand
440 their core area to meet their energy requirements. In other words, it is possible that the outer part of
441 the range may be more important for social behavior than for foraging. In chimpanzees (*Pan*
442 *troglodytes*) for instance, the size of home ranges reflects the abundance of resources; areas with
443 low abundance and high dispersal of food resources resulting in larger ranges (Dunbar 1988;
444 Herbinger et al. 2001) and those with local high abundance of food resources producing smaller
445 ones (Newton-Fisher 2003).
446 Due to the varying proportions of floodable, lowland and transitional forest in the owl
447 monkey study area, habitats differ in the quality and abundance of food resources they offer to the
448 various groups (van der Heide et al. 2012). Thus, one would expect to find higher local food
449 abundance in owl monkey groups with smaller ranges. However, despite pronounced differences in
450 the distribution of important tree species and food availability across four owl monkey ranges, there
451 was no evidence that groups with smaller ranges had more food available in their overall range (van
452 der Heide et al. 2012). The differences in food availability between the ranges of different groups
453 were more pronounced within outer range boundaries. The core areas were more similar to each
454 other, with important food species such as *Ficus* spp. being similarly abundant (van der Heide et al.
455 2012). The core areas were also comparatively more productive than the overall ranges, and
456 predictably produced food even during the dry seasons when overall food availability in the area
457 markedly decreased (van der Heide et al. 2012). During these dry seasons, core areas were similar in

458 fruit production for the different groups, and comparatively more productive than the overall group
459 ranges (Fernandez-Duque et al. 2013). The core areas had the smallest differences in food
460 availability among territories, which suggests that it is the quality of those that is the critical factor
461 for owl monkey feeding and foraging. Our findings support this argument, as we found the core
462 areas to be used almost exclusively, whereas the overall ranges overlapped considerably between
463 neighboring groups.

464 Furthermore, we found that core areas are only one third the size of the annual range, which
465 means that owl monkeys spent on average half of their time in less than half of their range. Such
466 intensive use of only a small part of the overall range is common in primates. Chimpanzees (*Pan*
467 *troglodytes*) spent 75% of the time in 35% of their range (Boesch and Boesch-Ackermann 2000) and
468 brown howler monkeys (*Alouatta guariba*) spent 50% of their time in only 10% of their range
469 (Agostini et al. 2010). Even though the notion of a 'core area' has been questioned (Barg et al. 2005;
470 Wray et al. 1992), our results show that, at least for owl monkeys, they exist as a biologically
471 relevant space.

472

473 *Site fidelity*

474 Owl monkeys made stable use of their ranges from one year to the next, and for almost a
475 decade. Generally, in any given year, groups occupied as much as 80% of the overall range they had
476 occupied the previous year. This finding provides some support for the prediction that owl monkey
477 ranges remain stable over several years as groups keep visiting the same locations of fruit trees
478 within their range. However, our method to determine site fidelity did not include the direction of
479 range shifts (Janmaat et al. 2009) or the number of years in which certain areas were used (Ramos-
480 Fernandez et al. 2013), which we propose as methods for future and more detailed analyses. The
481 high site fidelity observed for owl monkeys also fits well with overall abundance of food species
482 reported for the area (van der Heide et al. 2012), rendering range switches unnecessary in the

absence of pronounced social or ecological pressures. These results contribute to a small set of studies on site fidelity by primates conducted over periods of many years. Ring-tailed lemurs (*Lemur catta*) were found to occupy similar ranges even across generations (Jolly and Pride 1999; Mertl-Millhollen 2000), and grey-cheeked mangabeys (*Lophocebus albigena*) which, like owl monkeys, are highly frugivorous, also showed pronounced site fidelity with an overlap of over 60% over 10 years (Janmaat et al. 2009).

Naturally, site fidelity largely depends on the time scale at which it is analyzed. Even species considered site-faithful at relatively long temporal scales may exhibit seasonal movement patterns within their overall home range (Janmaat et al. 2009). Frugivorous primates often adapt their ranging behavior to local fruiting patterns; Sumatran orangutans, for example, follow peaks in fruit production along altitudinal bands within their overall range (Buij et al. 2002). To analyze seasonal movement patterns in frugivorous owl monkeys, movement analyses at finer temporal granularities, such as during dry or wet seasons, will be needed in the future; ideally those studies should be done together with accurate estimates of actual food availability in these seasonal ranges (Fernandez-Duque et al. 2013).

Range overlaps, monogamy and mate guarding

Following the mate-guarding hypothesis (Komers and Brotherton 1997), we predicted that for socially monogamous owl monkeys, groups would occupy non-overlapping territories. Our results do not provide direct support for the hypothesis since we found that on average half of their outer range overlapped with neighboring groups. Comparing range overlaps for owl monkeys with other monogamous species, we observed higher average overlap in our study (48%) than the 21% reported mean overlap for 26 socially monogamous primates (Lukas and Clutton-Brock 2013). In contrast to spatial overlap in the outer range parts, owl monkey groups occupied almost exclusive core areas that only overlapped minimally (10%) with other groups. In contrast with the high

508 overlap areas towards the outer range, the existence of such exclusively used spaces provides
509 support for the mate-guarding hypothesis. The high overlap of annual ranges and low overlap in
510 core areas indicates that owl monkey groups use the inner parts of the home range more exclusively,
511 while overlap occurs in the outer areas of the range. In those outer areas resident owl monkeys may
512 thus have potential access to more than one mating partner. Such potential access to mating partners
513 also exists for other socially monogamous and pair-living species (Dobson et al. 2010; Fietz et al.
514 2000; Palombit 1994). However, no extra-pair matings have been documented in owl monkeys
515 (Babb et al. 2011; Fernandez-Duque et al. 2008b).
516 The high overlaps in less used areas is in accordance with the findings that overlap zones in primate
517 ranges tend to be under-used (Wrangham et al. 2007). The core areas are thus where groups
518 maintain almost exclusive access to resources such as food, sleeping sites and mates by excluding
519 competition from other groups. In other words, it seems that for owl monkeys one can think of the
520 core area as a territory. Ongoing examinations of the spatial distribution of territorial behavior,
521 feeding and sleeping trees will allow us to test the potential function of the core area (Corley in
522 press; Savagian in press).
523 In the future it will be important to extend our analyses to consider in more depth the
524 temporal dimension of range use. Our analyses were almost exclusively on spatial overlap, but much
525 will be gained from detailed examinations of temporal overlap. We have observed that different
526 groups visit the same feeding trees that are located in overlapping areas. However, they mostly
527 visited during them during different times, although we documented few instances when groups
528 coincided in the same observation. These observations suggest that the overlap of these group ranges
529 is mostly spatial, and not temporal. Owl monkey groups may attempt to maximize access to
530 clumped high-quality feeding resources such as fig trees, while minimizing the possibility of inter-
531 group encounters that could lead to competition with same-sex individuals.

It is also possible that overlapping areas are important for dispersing individuals. When individuals move into new areas, they lack knowledge of important resources such as location of food and shelter. Dispersing red howler monkeys (*Alouatta seniculus*) for instance had a poorer diet than resident ones (Pope 1989 in Isbell and van Vuren 1996). In this context, overlapping areas between group ranges may provide dispersing individuals with the possibility to explore new social opportunities while, at least for some time, staying in a familiar area. In owl monkeys, all individuals of both sexes disperse, when they are approximately three years of age. The cost of dispersal is apparently high, given that it is the life stage when most animals die or disappear (Fernandez-Duque 2009). During dispersal some individuals were observed to linger in areas close to range boundaries (Fernandez-Duque 2009), which would indicate a gradual dispersal process away from the natal range. However, more detailed analyses are needed of movement paths of dispersing individuals with respect to group ranges to make inferences about the spatial aspects of the dispersal process in owl monkeys.

In conclusion, we have shown that owl monkey occupy home ranges of six hectares and core areas of two hectares. Both the within-group and between-group variability were high, but neither rainfall as an environmental variable or group size as a social variable were statistically significant predictors of this variation. Since we found no evidence that larger groups occupy larger areas than smaller groups, this indicates that food availability might be above a critical threshold for owl monkeys so that larger groups do not need to extend their foraging areas to meet their energy requirements. These results notwithstanding, we speculate that environmental and social factors might still have an influence, but that this influence occurs at temporal and spatial scales that we were unable to detect with our methods. Future studies could analyze these effects on ranging during smaller time periods, for instance during wet and dry seasons. We found that owl monkeys occupy ranges that stay stable over several years, which supports the prediction that in the absence of severe social or ecological pressure, owl monkey groups keep visiting the same locations of fruit trees

within their range. We found considerable overlap between neighboring groups and showed that this overlap occurs in the outer, less frequently used parts of their ranges. However, the overlap is more spatial than temporal, which maximizes access to clumped feeding resources in overlapping areas that are used at distinct times, while excluding other males from access to females in exclusively used areas.

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